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Open and closed cortico-subcortical loops: A neuro-computational account of access to consciousness in the distractor-induced blindness paradigm ☆

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A B S T R A C T

How the brain decides which information to process ‘consciously’ has been debated over for decades without a simple explanation at hand. While most experiments manipulate the perceptual energy of presented stimuli, the distractor-induced blindness task is a prototypical paradigm to investigate gating of information into consciousness without or with only minor visual manipulation. In this paradigm, subjects are asked to report intervals of coherent dot motion in a rapid serial visual presentation (RSVP) stream, whenever these are preceded by a particular color stimulus in a different RSVP stream. If distractors (i.e., intervals of coherent dot motion prior to the color stimulus) are shown, subjects’ abilities to perceive and report intervals of target dot motion decrease, particularly with short delays between intervals of target color and target motion.

We propose a biologically plausible neuro-computational model of how the brain controls access to consciousness to explain how distractor-induced blindness originates from information processing in the cortex and basal ganglia. The model suggests that conscious perception requires reverberation of activity in cortico-subcortical loops and that basal-ganglia pathways can either allow or inhibit this reverberation. In the distractor-induced blindness paradigm, inadequate distractor-induced response tendencies are suppressed by the inhibitory ‘hyperdirect’ pathway of the basal ganglia. If a target follows such a distractor closely, temporal aftereffects of distractor suppression prevent target identification. The model reproduces experimental data on how delays between target color and target motion affect the probability of target detection.

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1. Introduction

The global workspace theory proposes that only a subset of stimuli available in the outside world enter consciousness to become globally available for task-control processes (Baars, 1988). In this view, the 'global workspace' refers to a high-level processing and storage system that allows for the interaction of different specialized brain areas (cf. Baars, 2005). But how are visual stimuli gated into this processing and storage system? In a model proposed by Dehaene, Sergent, and Changeux (2003), the amount of stimulus activation is the critical factor. Their model explains why salient, well visible or attended stimuli are particularly amenable to becoming consciously available. Cognitive influences on conscious access, in contrast, cannot be explained by this model.

The neuronal determinants of stimulus-driven and cognitive influences on access to consciousness can be measured through distinct neuro-psychological paradigms. Stimulus-driven influences, for instance, are prominent in the attentional blink paradigm, where subjects are asked to detect target stimuli in a rapid serial visual presentation (RSVP) stream. In this paradigm, targets that follow previous targets by about 180–450 ms cannot be reliably detected by subjects (Raymond, Shapiro, & Arnell, 1992). Cognitive influences on access to consciousness, in contrast, have been investigated using the distractor-induced blindness paradigm (Niedeggen, Michael, & Hesselmann, 2012; Sahraie, Milders, & Niedeggen, 2001). In this paradigm, two separate RSVP streams are presented. In a global RSVP stream containing target two (T2) visual stimuli are presented in an annulus centered on a fixation point. In a local stream, presented in the center of the global stream, target one (T1) is included. By instruction, T2-like stimuli that occur after T1 presentation are to be detected as targets, while T2-like stimuli presented before T1 serve as distractors. Effects of distractor-induced blindness (i.e., non-detection of targets because of previous distractors) can be observed if the time interval between T1 and T2 (stimulus onset asynchrony, SOA) is below approximately 300 ms (cf. Sahraie et al., 2001). This blindness effect does not rely on an interaction of the two targets, in contrast to the attentional blink paradigm (Shapiro, 1994), but on cognitive effects of target-like episodes (i.e., distractors) preceding the onset of T1 (Hesselmann, Niedeggen, Sahraie, & Milders, 2006; Sahraie et al., 2001): these target-like episodes have been shown to result in a frontal negativity, cumulatively inhibiting target perception, as shown in a recent event-related brain potential (ERP) study (Niedeggen et al., 2012). This top-down *inhibitory* effect of distractors, i.e., their power to decrease the probability of getting conscious access to T2, is a unique characteristic of distractor-induced blindness. The specific neuronal mechanisms of this inhibition, however, remain speculative.

Empirical studies have shown an involvement of the prefrontal cortex (PFC; Demerzti, Soddu, & Laureys, 2013), sensory cortical areas (for a review, see Rees, Kreiman, & Koch, 2002), cortico-thalamo-cortical loops (Demerzti et al., 2013; Llinás, Ribary, Contreras, & Pedroarena, 1998) and the basal ganglia (BG) in consciousness (e.g., Balkin et al., 2002; Christensen, Ramsøy, Lund, Madsen, & Rowe, 2006; Gray, 1995; Kjaer et al., 2002; Mhuircheartaigh et al., 2010; Palmiter, 2011). Overall, therefore, it appears likely that there exists a widespread cerebral substrate of consciousness, in which different structures may fulfill different functions. The BG in particular are likely to exert modulatory control over consciousness with their direct, indirect and hyperdirect pathways. This should not be understood as implying that the BG are necessary for phenomenal awareness. Rather, they can enhance, but also suppress activity within the thalamus and cortex via these pathways, potentially contributing to the distractor-induced *inhibition* of access to consciousness in the distractor-induced blindness paradigm.

We here focus on the involvement of cortico-BG-thalamic loops in conscious perception, extending on our previous proposal that the BG are fundamentally involved in making contents globally available by their control over thalamo-cortical loops (Trapp, Schroll, & Hamker, 2012). We implemented a novel neuro-computational model that explains how conscious perception may evolve from reverberation of activity in closed cortico-subcortical loops. The model further predicts that BG pathways can control access to these closed loops based on top-down context information, determining which pieces of information will be allowed to reverberate. In contrast to the model by Dehaene et al. (2003) outlined above, thereby, our model explains cognitive inhibitory influences on access to consciousness. Via interconnected open cortico-BG-thalamic loops, BG pathways are additionally proposed to determine how conscious perception influences response selection in the motor cortex.

2. Methods

2.1. Model architecture

Based on anatomical observations (Haber, 2003), the model consists of two interconnected cortico-BG-thalamic loops (Fig. 1): A closed 'frontal' loop determines which pieces of information become consciously available, while an open 'motor' loop determines response selection. Each modeled nucleus and cortical area contains a population of artificial neurons. These neurons are interconnected in accordance with anatomical evidence (cf. Bolam, Hanley, Booth, & Bevan, 2000) as presented in Fig. 2.

Inputs presented to the model activate input cortical neurons that represent visual or categorical features, while responses are recorded in the motor cortex. BG pathways connect input cortices to the closed frontal loop, where stimulus-induced activity may reverberate, i.e., cause recurrent self-excitation. The closed frontal loop comprises the PFC which also is the origin of an interconnected open motor loop, where stimulus-induced activity is processed towards response